Multivariate hierarchical analyses of Early Jurassic Ostracoda assemblages

CARMEN ARIAS AND ROBIN C. WHATLEY

Palaeobiogeographic patterns of Early Jurassic ostracods from the northern and southern hemispheres (96 sections located in Europe, North Africa, Western Australia and North and South America) based on 243 species-level records document global patterns of distribution that can be compared to those previously published on ostracods from the European Epicontinental Sea and Tethyan and South Panthalassa areas. All described records of ostracods from both hemispheres spanning the Hettangian to Early Toarcian have been compiled and verified, and their patterns of origin and distribution have been interpreted. Jaccard coefficient of similarity was used to asses similarities among European, American and Tethyan ostracod shelf faunas. The numerical analysis shows a progressive longitudinal gradient in provincialism through the Early Jurassic, consistent with the northward drift of Tethyan ostracod faunas towards the European Epicontinental Sea and the southward movement of European taxa into Tethys and Panthalassa oceans. The spread of cosmopolitan species and extinction of endemic species, allied to the disappearance of geographical barriers, warmer climate conditions and rising sea levels can explain the reduction in ostracod diversity and the east-west provincialism throughout the Early Jurassic. Interchange between hemispheres, including bipolar distributions, are recognized from the Sinemurian time, pointing out that for most of the studied period, the climate worldwide was warm and tropical. □ *Early Jurassic, European Epicontinental Sea, ostracod, palaeobiogeography, palaeoceanography.*

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The study of Early Jurassic provincialism has focussed on few invertebrate groups, especially ammonoids, brachiopods and bivalves (Donovan 1967; Géczy 1973, 1984, 1985; Enay 1980; Dommergues 1982; Enay & Mangold 1982; Hallam 1984a; Crame 1986, 1991; Doyle 1987; Ziegler 1988, 1991, 1992; Riccardi 1991; Damborenea 1993). For a long time, the particular interest in this interval (from Hettangian to Toarcian) has been a reflection of the strong provincialism represented by the separation of Tethyan and Boreal provinces (Neumayr 1882, 1883; Uhlig 1911; Arkell 1956; Gordon 1970; Hallam 1975, 1983, 1984a; Bate 1977; Enay 1980; Copestake & Johnson 1984; Cariou *et al.* 1985; Liu *et al.* 1998). Since the 1970s it has become clear that various microfossil biogeographic provinces could also be distinguished (Gordon 1970; Bate 1977; Lord 1982, 1988; Herrig 1988; Whatley 1988; Bucefalo-Palliani & Riding 2003; Van de Schootbrugge *et al.* 2005).

The first tentative suggestion of the existence of Jurassic ostracod provincialism is that proposed by Bate (1977), who recognized five provinces based on the distribution of the Early Jurassic Ostracoda: the European, Tethyan, North African, American Province and East African. The European Province expanded from Newfoundland to the Ukraine and from Greenland to the northern margin of the Tethys area, including the Iberian Peninsula. The Tethyan Province extended from eastern Canada to North-West Africa. The palaeobiogeography of Early Jurassic ostracods of southern Europe is much less clear, because this latter province has a less complete record and its existence is more difficult to establish at least during this period. A recent study demonstrates an important change in Early Jurassic ostracod provincialism (Arias 2007b) and shows that provincialism was only outstanding from the Hettangian to middle Toarcian. It is not possible, however, to distinguish between the European and Tethyan provinces, at least since the *Serpentinus* Zone (Toarcian), because no particular ostracod species is present in only one ostracod province.

The aim of the present paper is to discuss: (1) the similarity between European, American, African and

Western Australian ostracod assemblages; (2) to compare the marked ostracod provincialism with the provincialism of various fossil groups; and (3) to relate ostracod distribution patterns to palaeoclimatic and palaeoecological conditions.

Materials and methods

Before the distribution pattern of the different ostracod taxa can be analysed, knowledge of the palaeogeography is required. In the most generally accepted reconstructions, we see a world dominated by the presence of a single supercontinent, Pangaea, surrounded by a giant ocean, the Panthalassa Ocean (Dewey *et al.* 1973; Biju-Duval. *et al.* 1977; Owen 1983; Dercourt *et al.* 1985; Ziegler 1988, 1991, 1992; Veevers 2004). This supercontinent comprised two large landmasses: one southern continent known as Gondwana (South America, Africa, India and Antarctica) and another northern continent called Laurasia (Europe, North America and Southeast Asia). At the beginning of Jurassic, the European continent, sited in central Laurasia (Fig. 1) was covered by an epicontinental sea with restricted basins among an archipelago of islands (Hsü 1971; Thierry 1976; Smith 1983; Cariou *et al.* 1985; Bassoullet *et al.* 1991, 1992; Meister & Stamfly 2000; Ziegler *et al.* 2000). In order to examine ostracod palaeobiogeographical patterns, we focused on 19 areas and 96 sections (Fig. 1, Table 1).

Much of the published literature dates from the last 30 years, and contains considerable duplication. Thus, this work involved a revision of each marine ostracod species, considering only those species, which have been well illustrated in the literature, therefore avoiding doubts in their identification. For each Early Jurassic stage (Hettangian, Sinemurian, Pliensbachian and earliest Toarcian) we produced a similarity symmetrical matrix, following Q-mode analysis (Henderson & Heron 1976; Keesey & Whitaker 1976; Pielou 1979; Janson & Vegelius 1981; Digby & Kempton 1987). Inequality in sampling effort can influence species occurrences and richness estimates, and consequently, this paper only works with species composition not species richness. Following this intention, Jaccard's similarity coefficient (Jaccard 1912) was chosen because: (1) it ranges from zero to one; (2) is independent of double absence; (3) emphasises presence instead of absence; and, (4) it not vulnerable to differences in sample size (Morisita 1959; Cheetham & Hazel 1969; Goodall 1973, 1978; Gower 1975; Baroni-Urbani & Buser 1976; Hohn 1976; Huhta 1979; Lamont & Grant 1979; Wolda 1981; Hubalek 1982; Archer & Mapples 1987, 1989;

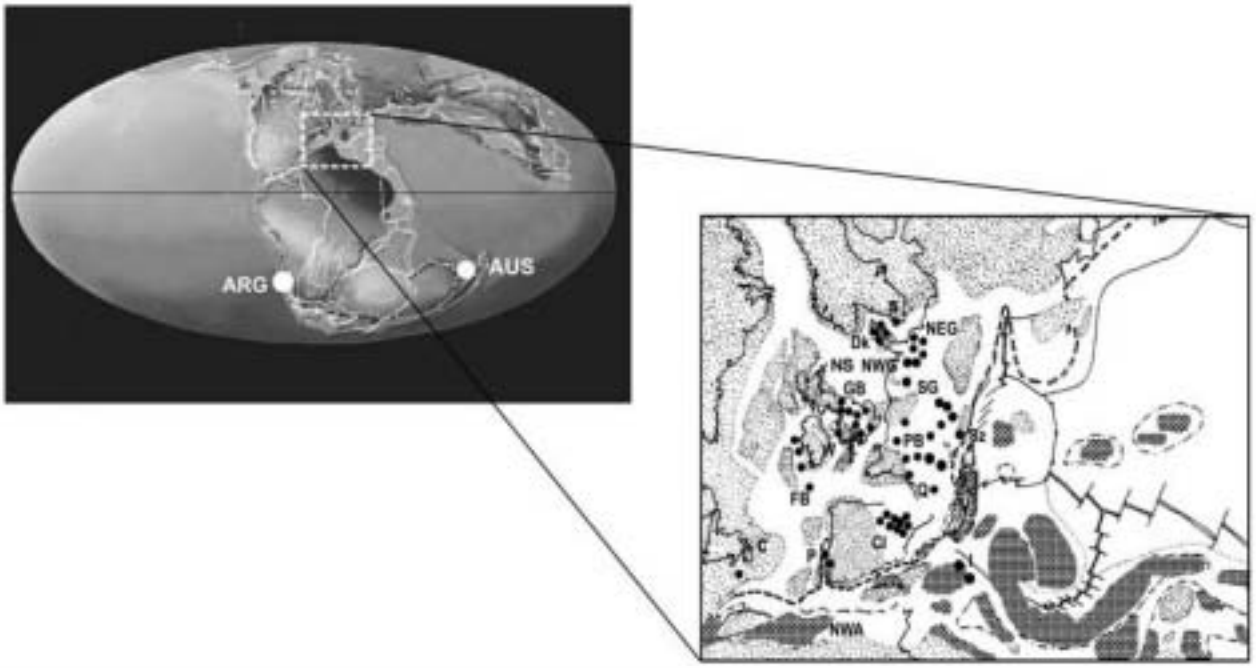

Fig. 1. Location of the studied areas (palaeogeographical reconstruction after Ziegler, 1988 and Bassoullet *et al.* 1992). ARG, Argentina; AUS, Western Australia; C, Canada; CI, Cordillera Ibérica; Dk, Denmark; FB, Fastnet Basin; GB, Grand Banks; I, Italy; NWA, North West Africa; NEG, Northeast Germany; NS, North Sea; NWG, Northwest Germany; PB, The Paris Basin; P, Portugal; Q, Quercy, France; SG, Southern Germany; S, Skøne, Sweden; SZ, Switzerland; and, W, Wales (Plate tectonic maps and continental drift animations modified from Scotese (2001).

Table 1. List of important and/or well-known ostracod localities worldwide

Areas	References	Studied localities
	Drexler 1958	Siebeldingen (Rheinland-Pfalz)
	Pietrzenuk 1961	Dobbertin (Mecklenburg-Vorpommern) and Eisenach (Sachsen)
	Dreyer 1967	Brandenburg
Northeastern Germany (NEG)	Herrig 1969a,b	Greifswald (Mecklenburg-Vorpommern)
	Herrig 1979, 1980, 1981a, b, c, 1982a, b, 1985	Thüringen
	Triebel & Bartenstein 1938	Baden (Niedersachten)
	Triebel & Klingler 1959	Hannover (Niedersachten)
Nortwestern Germany (NWG)	Gramann 1963	Weseker Sattel (Nordrhein-Wesfalen)
	Malz 1971	Niedersachten
	Ohm (Fischer *et al.*), 1984	Empelde (Niedersachten)
	Fischer *et al.* 1986	Hannover (Niedersachten)
	Fischer 1961a, b, 1962	Baden-Württemberg
	Klingler 1962	Baden-Württemberg
	Beher 2004; Beher *et al.* 2001	Baden-Württemberg
	Malz 1975	Baden-Württemberg
	Knitter 1983, 1984	Baden-Württemberg
Southwestern Germany (SWG)	Knitter & Ohmert 1983, 1986	Baden-Württemberg
	Knitter & Riegraf 1984	Baden-Württemberg
	Riegraf 1984, 1985	Baden-Württemberg
	Harloff 1993	Baden-Württemberg
	Harloff & Jäger 1994	Baden-Württemberg
	Beher 2004; Beher *et al.* 2001	Southern Germany
Canada (C)	Exton & Gradstein 1984	Grand Banks, Newfoundland
Celtic Sea-Fasnet Basin-Porcupine (FB)	Ainsworth 1986a, b, 1987, 1989	Fasnet Basin
	Ainsworth & Horton 1986, 1987	Fasnet Basin
	Ainsworth *et al.* 1987	Fasnet Basin
North Sea	Malz & Nagy 1989	North Sea
	Ainsworth 1990	Porcupine, Slyne, Evris and Donegal
Danish Embayment, Denmark (Dk)	Michelsen 1975	Danish Embaymen
Skane, Southern Sweden (S)	Sivhed 1980	Skane
	Apostolescu 1959, 1961	Paris Basin
	Apostolescu *et al.* 1961	Paris Basin
	Bizon 1960, 1961	Basse Normandie
	Bizon & Oertli 1961	Lorraine
	Cousin & Apostolescu 1961	Ardennes
	Champeau 1961	Paris Basin
	Oertli 1961, 1963, 1985	Paris Basin
Paris Basin, France (PB)	Oertli & Grosdidier 1961	Paris Basin
	Magné & Malmoustier 1961	Thouars
	Magné *et al.* 1961	Thouars
	Maupin 1978	Vendee
	Dêpeche 1985	France
	Donze 1985	France
	Riegraf 1985	Truc de Balduc
	Bodergat *et al.* 1991	Paris Basin
	Bodergat & Donze 1988	Paris Basin
	Cubaynes & Faure 1981	Quercy
Quercy, France (Q)	Cubaynes 1986	Quercy
	Andreu *et al.* 1998	Quercy
	Cubaynes & Ruget 1985	Quercy
	Lord 1974, 1978, 1988	Great Britain
	Bate & Coleman 1975	England
Great Britain (GB)	Lord & Bown 1987	Dorset and Isle of Wight
	Boomer 1991	Mochras, Wales
	Boomer 1992	Ilminster, southwestern England
Italy (I)	Lord 1988	Strettura
	Arias 1993	Umbria
	Exton 1979	Zambujal
Portugal (P)	Exton & Gradstein 1984	Zambujal
	Boomer *et al.* 1998	Zambujal
northwestern Switzerland (Sz)	Richter 1987	Basel
	Harloff & Jäger 1994	North Tyrol
Argentina (ARG)	Ballent 1987, 1991, 1992	Neuquén
Australia (AUS)	Lord *et al.* 1993	Western Australia
Leg 79, site 547 (off-northern Africa) (NA)	Bate *et al.* 1984	Leg 79, site 547
	Arias 1989, 1991, 1995	Cordillera Ibérica
	Arias & Comas-Rengifo 1992	Cordillera Ibérica
Cordillera Iberica Spain (SP)	Arias *et al.* 1992	Cordillera Ibérica
	Arias & Lord 1999a,b	Cordillera Ibérica

Kenkel & Booth 1987; Koch 1987; Magurran 1988; Mapples & Archer 1988; Hengeveld 1990). Jaccard's Index is calculated by dividing the number of species found in both of two samples (c) by the number found in only one sample and the other (a and b) and then multiplying by 100:

$$JI = c/(a + b + c) * 100$$

where c is the number of species in common; a is the number of unique species to community 1; and b is the number of unique species to community 2.

This paper considers the agglomerative clustering method UPGMA (Unweighted Pair Group Method with Arithmetic mean) because it provides an unweighted arithmetic average between individuals (Hazel 1970; Anderberg 1973; Sneath & Sokal 1973; Everitt 1980; Romesburg 1984; Podam 1989; Shi & Waterhouse 1990; Shi 1993). All analyses were done using the statistical software package NTSYS 2.02 (Rohlf 1997).

Results

The classification of the 19 areas analysed in terms of their similarities to the ostracod assemblages is shown in Figure 2A–D. For the Hettangian (Fig. 2A), the analysis shows two main groups that reveal a major separation between the north and central and the southern European faunas. With the exception of Western Australia, resemblances generally decreased as the geographical distances to the Tethys Ocean increased. Considering this gradient of likenesses, we used two threshold values to discuss the groups formed at different levels. By using a conservative value of 0.30 similarities, a large group is formed that encompasses the Paris Basin, central England, Wales and southern Germany. Additionally one small group is distinguished, comprising Northeastern Germany and Portugal, which implies that the members of these pairs are equally similar to the Western European ostracod assemblages. Within the main group a compact core (British and the Paris basins) is differentiated, which is included by entities having similarities between them of at least 0.40. Southern Germany is excluded from this core, thus it is the least related to the remaining entities, which constitutes central Europe. Contrary to our expectations based on our previous knowledge of Portuguese fauna (Arias 1995) using this threshold we left Portugal out of the main group. The second group includes European area located on the northern margin of the European Epicontinental Sea (Danish Embayment, southern Sweden and the Fastnet Basin).

Similarities among studied assemblages for the Sinemurian are represented by the dendogram. Figure 2B shows a division between all northern and central and southern European areas. The grouping of the analysed entities was notably modified when we used the highest similarity value (0.50). At this level, two well-defined groups are formed, and only the North Sea and Italian assemblages remained as isolated entities. The main group, located in the upper section of the dendogram, comprises all entities located in northern (Swedish Danish, northern German assemblages) and central European areas (southern Germany and the Paris Basin), which together correspond to the northeastern margin and central areas of the European Epicontinental Sea. The second group includes the British basins (as far north as the Fastnet Basin, as well as western British basins, both located on the northwestern margin of the European Epicontinental Sea), Quercy and Northwestern Africa basins (together situated on the southwestern margin of the European Epicontinental Sea). Surprisingly, Portuguese assemblages did not cluster with the second one (British Basin-Quercy-NW Africa), forming an independent group (Fig. 2B). Western Australia is associated to both clusters.

For the Pliensbachian (Fig. 2C) two major clusters were obtained. With the exceptions of Western Australia and Canada, similarities reduced as the spatial distances to central European Epicontinental Sea increased. Bearing in mind this similarity, we used two threshold values to examine the clusters formed at different ranks. By using the value of 0.40 similarity, an important group is formed that includes the Cordillera Ibérica (Spain), Quercy (southern France), Zambujal (Portugal) and the Fastnet Basin (southwest Ireland). Additionally two small groups are distinguished, one comprising the Cordillera Iberica–Quercy, and the other, Portugal and Fastnet Basin. Within the main group a compact centre is differentiated, within which is included entities (Cordillera Ibérica and Quercy) having similarities between them of at least 0.78. The other main group, located in the lower part of the dendogram, comprises all entities located in German and Danish basins, which correspond approximately to the northeastern margin of the European Epicontinental Sea. Contrary to our expectations, using this threshold left central England out of the both main groups and formed a free cluster related to the central and southwestern European assemblages, showing the high similarity values to the Cordillera Ibérica. Swiss (Sz) and Italian assemblages (I) are separated from the remaining areas. Canadian assemblages show a minimum similarity with the rest of studied area. The biotas of Western Australia and Argentina make up independent

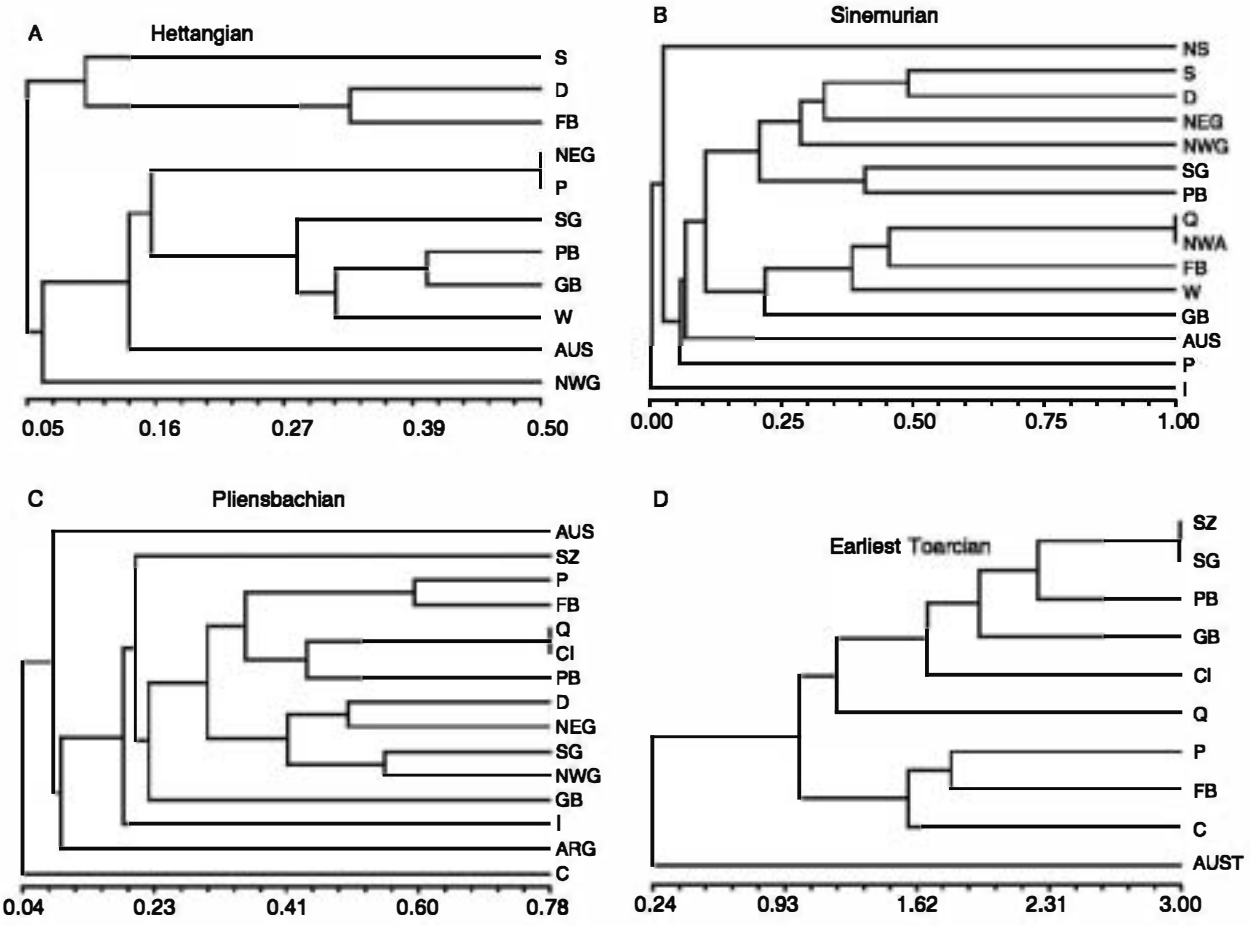

Fig. 2. Dendogram of UPGMA analysis based on 19 loci for: A, Hettangian; B, Sinemurian; C, Pliensbachian; and, D, Early Toarcian. The scale indicates the grade of similarity as determined with the Jaccard similarity coefficient. Abbreviations as in Figure 1.

branches. Argentinean faunas show higher values of similarity with European than Western Australian does (Fig. 2C).

The Western Australian area exhibited the lowest similarity relative to the rest of the sites during the earliest Toarcian (Fig. 2D). The first level shows two large groups: one comprises the western and central European assemblages (Cordillera Ibérica, the Paris Basin, Quercy, southern Germany, Switzerland and central England), and the other group sites along the western margin of the European Epicontinental Sea comprise assemblages from Portugal, the Fastnet Basin and eastern Canada. The highest similarity within the central European areas was between southern German and Swiss assemblages, showing both the highest faunal similarity with central England. The areas of Zambujal, Portugal and the Fastnet Basin, in the western part of European Epicontinental Sea , form a group with considerably high similarity, and although are physically closest to the Cordillera Ibérica, they are included in a different cluster. Finally, the Western Australia assemblages are the least similar to the European assemblages.

Compiling all the results demonstrates the evolution of the similarity between Early Jurassic ostracod assemblages. At the beginning of the Early Jurassic (Fig. 3A), the cluster analysis shows an initial division between northern and central European ostracod assemblages along the North Sea. This boundary during the Sinemurian (Fig. 3B) situates along a line, which passes through central Europe, between British and the Paris Basin and German areas. The main transformation took place during the Pliensbachian (Fig. 3C), with the boundary located between eastern (German and Danish basins) and western European basins (French and the Iberian Peninsula basins). The boundary is now located eastwards of the previously described position, with British assemblages maintaining as an independent group. During the earliest Toarcian, Tenuicostatum Zone, the boundary line experiences a distinctive westward movement and the Portuguese and the Fastnet Basin ostracod

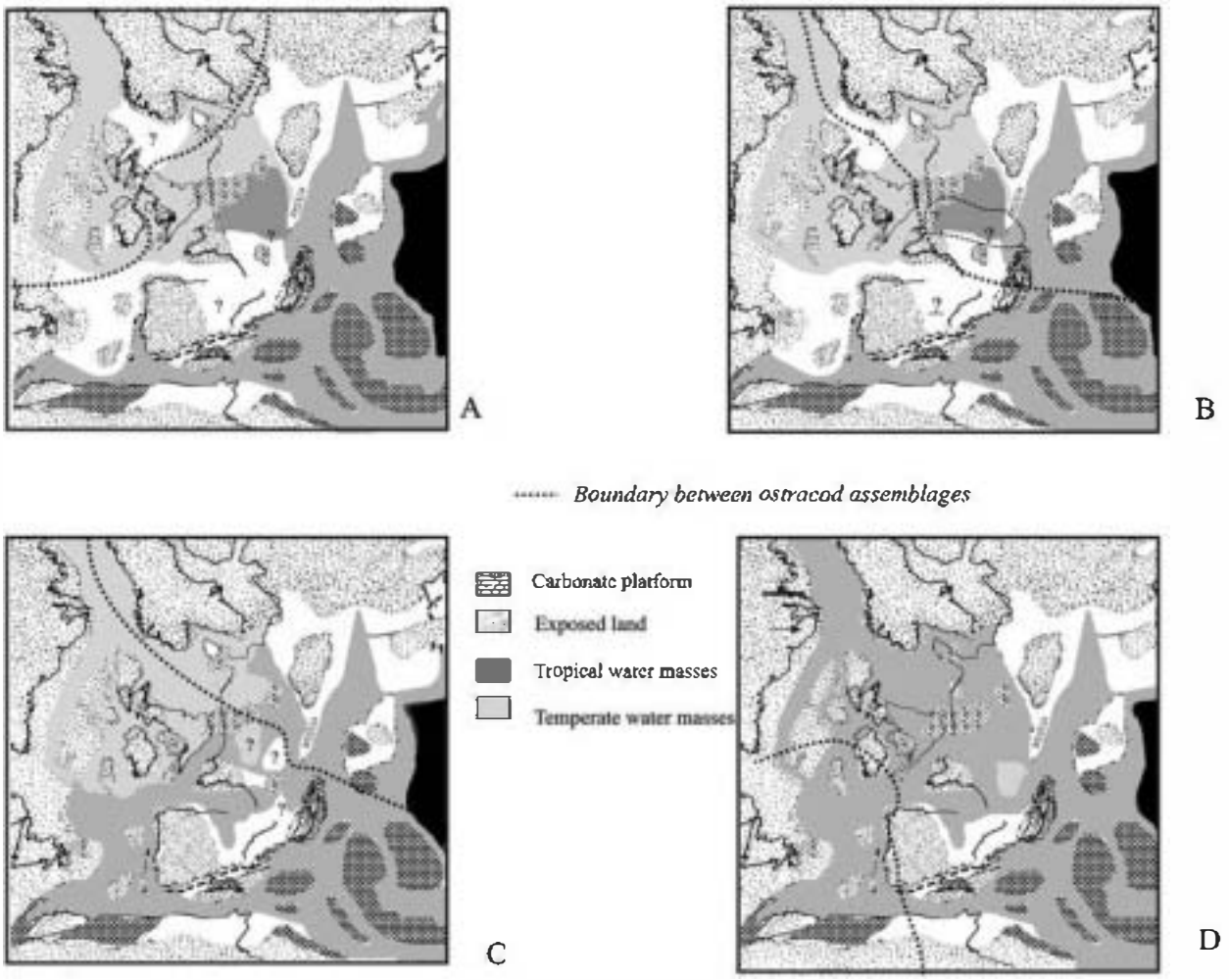

Fig. 3. The position of the boundary among major similarity clusters of ostracod assemblages. A, Hettangian; B, Sinemurian; C, Pliensbachian; and, D, Early Toarcian.

assemblages became an independent unit from the rest of European areas (Fig. 3D). The general results of the cluster analysis indicate a progressive translation of the border during the Early Jurassic.

Discussion

Ostracoda are tiny crustaceans, laterally compressed, enclosed within a bivalved carapace. Their longevity, renowned diversity of forms and limited dispersal capability make this group a potential source of the information on history of Early Jurassic seas. The majority of Early Jurassic ostracods were neritic and most of them specialized in shallow-marine environments (Arias & Whatley 2004). In a palaeoecological perspective, ostracod palaeobiogeographers have used their patterns of distribution to infer the ecological role of several factors such as, depth, temperature, pH, light, etc. (Elofson 1941; Hallam 1969, 1978, 1985; Gordon 1970; Hazel 1970; Stevens 1973; Wood & Whatley 1994; Arias & Whatley 2004).

The causes of palaeozoogeographical differentiation are complex and often difficult to understand. In order to elucidate the causes, both ecological and historical factors must be taken into account, together with the phylogeny of the fossil group being studied. This is difficult for the Early Jurassic, because of our limited knowledge of the details of Jurassic marine environments. Evidence for unusually warm temperatures during the early Jurassic are frequently cited in palaeoclimatological, palaeontological and geological studies. In an ecological context, palaeobiogeographers have used spatial patterns of distribution to infer the ecological role of several factors such as temperature, depth, pH, light, etc., (Arias & Whatley 2004). Nevertheless, when we work on fossils, our considerations must incorporate new aspects, such as: palaeogeographical reconstructions, phylogenetic relationships and those taphonomic processes that

could have affected palaeobiogeographical results. In this study, the presence of different physical barriers (emerged lands, ocean currents, deep water and water chemistry), water temperature changes, sea level variations and changes in ocean circulation are considered as forcing agents of the palaeogeographical evolution during the Early Jurassic.

Depth and water temperatures

Benthonic ostracod species of the platform environments are characterized by their broad geographical ranges but show certain restriction in relation on the depth. Depth, in itself, is not the most important factor because its influence lies principally in its effect on other factors, such as, the water temperature, density or light intensity. Temperature has always been regarded as one of the most important factors in controlling the distribution of ostracod species (Whatley 1988) because it controls such factors of ostracod ecology, such as breeding season, abundance of individuals, food supply, size, etc.

Early Jurassic ostracod faunas reached their highest diversity in mid-shelf, warm-water tropical and subtropical environments, where shallow carbonates were deposited (i.e. the area between the line, which contains the Bohemian, the Rhenish-London-Brabant and the Iberian massifs, and the Irish Massif; or warm carbonate platforms along the northwestern African coast). Meanwhile deep-water clastic sequences, deposited at higher latitudes in cooler water settings (clastic deposits located between the Fennoscandian High and the Bohemian Massif; and the Lusitanian and the Fastnet basins) are characterized by lower diversity assemblages. This factor could partially explain why Irish and Portuguese ostracod assemblages form an independent cluster during the Pliensbachian–Toarcian transition (Arias 2007b).

Conventionally, the water temperature and salinity are considered as the major controlling factors on local distribution of invertebrate faunas (Donovan 1967; Gordon 1970, 1975; Howarth 1978; Brown 1988; Whatley 1988; Riccardi 1991; Rosenzweig 1995; Rohde 1998; Gaston 2000). Jurassic climate is characterized by being warmer and more equable than the present climate (Frakes 1979; Parrish 1982; Parrish & Curtis 1982; Hallam 1984b, 1994; Frakes *et al.* 1992; Scotese 2001). These ideas are in disagreement with recent findings that suggest the occurrence of short cold episode during the Early Jurassic, particularly at the Pliensbachian–Toarcian transition (Rosales *et al.* 2004; van de Schootbrugge *et al.* 2005; Arias 2007a). Climate-sensitive sediment distribution (of such lithologies as coal, evaporite and carbonate) provides a particularly useful means of interpreting Early Jurassic palaeoclimates (Robinson 1973; Gordon 1975; Frakes 1979; Parrish 1982; Hay *et al.* 1982; Manspeizer 1988; Frakes *et al.* 1992). Frakes *et al.* (1992) categorized Early Jurassic marine environments in a series of regional climate zones by integrating global lithological data distribution. Following this zonation, temperate and humid conditions would dominate across the northern margin of the European Epicontinental Sea and Western Australia; subtropical climate conditions in the middle of the European Epicontinental Sea and southern Argentina; and tropical climate conditions along the North Africa coast and the Iberian Peninsula. Palaeontological proxies also confirm the existence of this equator-to-pole surface-temperature gradient, with temperate water from European Epicontinental Sea and a subtropical and tropical Tethys Ocean (Vakhrameev 1964; Hallam 1972, 1975; Frakes 1979; Rees *et al.* 2000; Arias & Whatley 2004; Arias 2007a, b).

Because the reliability of the available oxygen isotope measurements is questionable, climate simulations models have computer-generated sea surface temperature (Kutzbach & Gallimore 1989; Chandler *et al.* 1992). Sea surface temperature simulations indicate the presence of warm polar waters (seasonal range between 3.5–9.5°C), a low equator-to-pole temperature gradient of 22.2°C, and an east-west equatorial temperature gradient (from 25°C in the eastern Panthalassa, to 32°C in the west Tethys). Climate models indicated that the European Epicontinental Sea was a tropical sea (with sea surface temperature of up to 25°C year round, reaching 15°C in autumn and less than 10°C in spring) and that Western Australia and Argentinean areas exhibited a similar sea surface temperature range (18–24°C) (Kutzbach & Gallimore 1989; Chandler *et al.* 1992). This thermal gradient across the central Pangaea is also explained by the development of the break-up of the supercontinent Pangaea, and the topography of the new proto-Atlantic rift (Gordon 1975; Manspeizer 1988). A result of this new topography, strong monsoonal conditions could have developed (Barron & Washington 1982; Parrish & Curtis 1982; Fleming 1983; Crowley *et al.* 1989; Kutzbach & Gallimore 1989; Kutzbach, *et al.* 1990; Chandler, *et al.* 1992; Barron *et al.* 1994; Chandler 1994; Arias 2007a).

Therefore, the majority of Early Jurassic palaeoclimatic data show the existence of a latitudinal thermal gradient in both hemispheres. Ostracod assemblages seem to be confined to distinct biogeographical areas, reflecting water masses with a particular temperature regime, e.g. large, thick-shelled ornamented cytheroid dominate mid- and high-latitudes, meanwhile ornamented and smooth healdioids and bairdioids, and cytherellids prevail in low latitudes. Initially, this

sharing out could correspond to temperate and warm-water ostracod faunas, respectively. However, the ostracod assemblages distribution is neither spatially constant nor shows a progressive latitudinal trend in the course of the Early Jurassic. If global temperature changes were fast and extreme, their effect would be to shift water masses and the associated ostracod faunas should move with them. Only the existence of a weak sea surface temperature latitudinal gradient from the Hettangian to earliest Toarcian in the European Epicontinental Sea might explain the non-existence of a latitudinal control over ostracod provincialism, the northward expansion of the warm Tethyan fauna to the more hostile unstable European Epicontinental Sea environment and the southward movement of European cytheroids. These movements could result in the combined presence of both assemblages across the whole European Epicontinental Sea and would explain the ostracod associations illustrated all through the Hettangian, Sinemurian and Pliensbachian similarity dendograms (Fig. 2A–C) and the lack of a latitudinal gradient, at least since the Sinemurian.

Therefore, Early Jurassic ostracod palaeobiogeography suggests that the water temperature was certainly a limited factor in the distribution of ostracods, although is difficult to demonstrate its effects. An increase of the environmental stability in the European Epicontinental Sea may explain why the Tethyan faunas did not had a limited northward during the Early Jurassic, the free movement of ostracod fauna across the whole studied area and the absence of a latitudinal provincialism. Although more information is needed in order to make interpretations less speculative, the effects of thermal variations in determining cycles of shrinking and expansion of the biogeographical distribution of ostracod diversity cannot be disregarded.

Sea level changes and physical barriers

The Jurassic was a time of major sea-level transgressions and regressions in both regional and global scales. Another important environmental factor for explaining ostracod movements is the sea-level change. Low stands reduce open seaways and spread of the ostracod faunas; meanwhile high sea levels facilitate faunal exchange, what would lead to an increase in overall diversity and extensive distribution of the fossil assemblages (Jablonski 1980; Meister & Stamfly 2000). During the Early Jurassic, there was a transgressive trend with deepening episodes in the late Hettangian, mid-Sinemurian, latest Sinemurian, mid-Pliensbachian, late Pliensbachian, mid-Toarcian and latest Toarcian (Vail *et al.* 1977; Hallam 1978, 1984a, 1988; Haq *et al.* 1987, 1988; Hardenbol *et al.* 1998; Meister & Stamfli 2000; Gómez & Goy 2002, 2005). These curves show episodic falls in sea level in the Late Triassic, Early Hettangian, Late Pliensbachian and mid-Toarcian (Vail *et al.* 1977; Hallam 1984a; Haq *et al.* 1987, 1988; Roth 1987; Hardenbol *et al.* 1998; Meister & Stamfli 2000; Gómez & Goy 2002, 2005). For the beginning the Jurassic, we recognize two main faunal clusters (Figs 2A, 3A). The boundary between both ostracod assemblages would set around the British Isles during the Hettangian. The limit moves eastward to reach central Europe during the Sinemurian (Fig. 3B) separating western (British basins) and central European (French and German basins) assemblages. A new eastward progress of the boundary shifts apart central (German basins) and northwestern European (British and French basins) ostracod assemblages during the Pliensbachian (Fig. 3C). Early Toarcian (Fig. 3D) reunites all European ostracod assemblages, but the most western extreme area (the Fastnet Basin, the western Portugal and the eastern Canada). Initially, it would be possible to relate all these movements, go forward and draw back, of the boundary with eustatic changes. Transgressive episodes could be linked to the eastward movement of the boundary (i.e. during the Sinemurian and Pliensbachian), and regressive episodes to the westward progress of the boundary (i.e. at the beginning of Toarcian). Thus, sea level changes could be a dominant factor controlling ostracod diversity and migration.

Explanations for the distribution pattern of marine ostracod include, in addition to changes in temperature and eustatic sea level, the presence or absence of physical barriers (such as landmasses or deep water) as potential factors governed the ostracod distribution by means of opening or closing of the communication routes between basins. Barriers, such as shallow carbonate platforms or emerged land belts along the southern part of the European Epicontinental Sea (i.e. the Briaconnais and Corso-Sardinia blocks or the Balears and Pre-Betic platforms), might have also acted as a barrier insulating the European Epicontinental Sea from the Tethys Ocean (Almeras & Elmi 1987). Only a few areas (areas between the Lower Austroalpine and South Calcareous Alps; across the Balcony Mounts; the Burgundy area or between the Sub-Briaconnais and the Lower Austroalpine areas) may have worked temporally as a passage, at least from the Late Sinemurian to Pliensbachian (Dommergues & Meister 1991; Meister & Stamfly 2000). The opening of these interchanges seaways would be responsible for the north-south direction of the boundary during Sinemurian and Pliensbachian (Fig. 2B–D) and the pattern of ostracod migration

(closest areas to these entrance areas, i.e. German, Swiss and French are very similar). The same can be said for the other entrance route, the Iberian-Moorish Strait, between North African and British basins during the Pliensbachian (Dommergues & Mouterde 1980; Dommergues 1982; Enay & Mangold 1982; Cariou *et al.* 1985), would explain the highest similarity among western European and African ostracod assemblages during the Pliensbachian (Fig. 2C).

However, the question remains as to why ostracods did not spread longitudinally. The answer could be the presence of physical barriers and seaways. For example, the opening of the Poitou Strait between the Aquitaine and Paris basins during the Late Pliensbachian (Gabilly 1976; Galbrun *et al.* 1994) not only facilitated a new access for faunal interchange between Quercy and the rest of central European basins but also would explain the similarity between French assemblages (the Paris Basin and Quercy) during the Pliensbachian–Toarcian boundary (Fig. 2C, D). Nevertheless, the most remarkable aspect of cluster results was that during the Pliensbachian (Fig. 2C), British assemblages maintained an independent position relative to the rest of central European areas and that German basins were shifted to French basins assemblages. The response would be the presence of some barrier around the London-Brabant Massif (Moreton-in-Marsh and Market-Weighton thresholds) that kept British basins in isolation, preventing faunal interchanges between northern German and southern British basins (Ager 1956; Donovan 1967; Howarth 1973; Mégnien 1980; Dommergues 1982; Enay & Mangold 1982; Meister & Stamfly 2000). Their posterior total opening would explain the westward movement of the boundary during the earliest Toarcian (Fig. 2D).

The most significant was the aperture of the Hispanic Corridor (Smith 1983), right through the present Strait of Panama, which could have allowed, since the Pliensbachian, the movement of European and Tethyan ostracod forms into the Panthalassa ocean (Damborenea 2000; Arias 2006). This new passage might explain a new generalized westward expansion of the western European Epicontinental Sea ostracod faunas to the Argentinean basins, southeast Panthalassa Ocean (Boomer & Ballent 1996; Arias 2006), and could be the root for the minor cluster, which comprises Portuguese, Canadian and Irish ostracod assemblages during the earliest Toarcian (Fig. 2D).

Water masses and ocean circulation change

The importance of marine currents in governing faunal migration is out of doubt. Several authors have attempted to reconstruct the palaeocurrent patterns of the Jurassic oceans from the research on the rate and routes of fossil migration (Ager 1975; Enay 1980; Arias & Whatley 2004; Arias 2007a). Palaeoceanographic models are presently the most used for simulating Early Jurassic ocean-surface circulation (Parrish & Curtis 1982; Parrish *et al.* 1982; Crowley *et al.* 1989; Kutzbach & Gallimore 1989; Kutzbach *et al.* 1990; Chandler *et al.* 1992; Barron *et al.* 1994; Chandler 1994; Scotese & Summerhayes 1986; Arias 2007a) (Fig. 4A, B). Many authors have postulated the existence of Arctic/Boreal and Tethyan currents flowing in opposite directions currents, until they collided in the northern part of the European Epicontinental Sea contributing to the Boreal/Tethys provincialism (Ager 1975; Fürsich & Sykes 1977; Arias 2007a). This collision of currents could cause the division outlined in the Figure 2A.

Arias (2007a) explained in the broader context of the European Epicontinental Sea deep oceanic circulation, the movements of European ostracods during the Pliensbachian–Toarcian boundary. She combined faunal, lithological, salinity and temperature distribution, proposing an integrated threefold classification of water masses (tropical, subtropical and temperate). In this model, the deep-water circulation would be of an estuarine type with warm water from the Tethys flowing northwards at depth to the European Epicontinental Sea and superficial cold and freshening water flowing out from the European Epicontinental Sea to the Tethys Ocean (Arias 2007a). As a result, the deep water filling the European Epicontinental Sea was warmer, what is reliable with estimated palaeotemperatures and the temperature gradient between the northern latitudes and the tropics. These environmental conditions allow the free movement of ostracod faunas through the European Epicontinental Sea, with the entry of Tethyan faunas along the southern margin of the European Epicontinental Sea and the southward movement of the European ostracod faunas (Fig. 5). The cluster analysis of the Early Jurassic ostracod faunas also reveals a high degree of similarity between South America, Australia and western and central Europe. Since Australian faunas are similar to central Europe assemblages, an open communication along the western Tethys, aided by eastward currents was suggested by Arias (2006). Ostracod assemblages from central Argentina show higher similarity to western European Epicontinental Sea (Portugal, Grand Banks, the Fastnet Basin, and Wales) and North Africa than to central European assemblages. This assumption would indicate an east-west migration of the European ostracod faunas across the Hispanic Corridor, since at least the Pliensbachian–Toarcian (Boomer & Ballent 1996; Arias 2006).

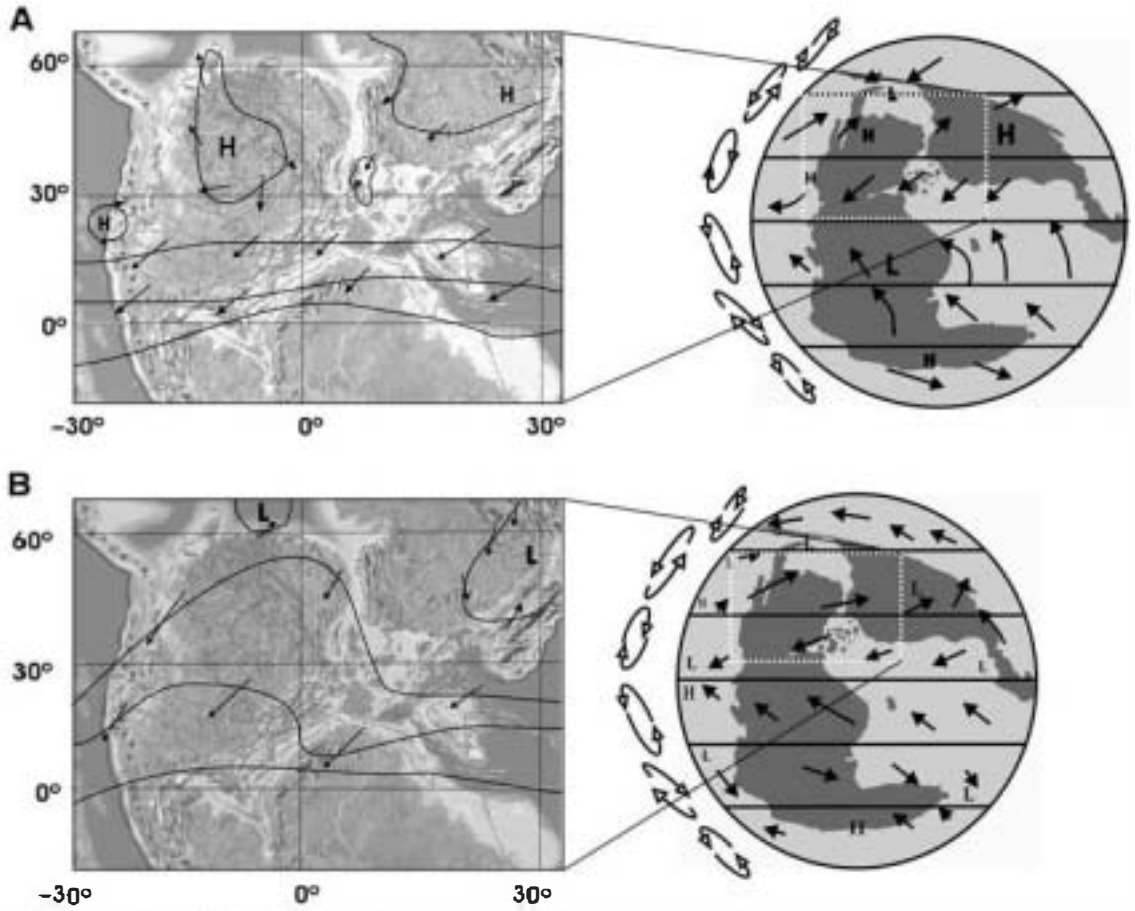

Fig. 4. Early Jurassic atmospheric circulation in the northern Hemisphere. A, winter; and, B, summer.

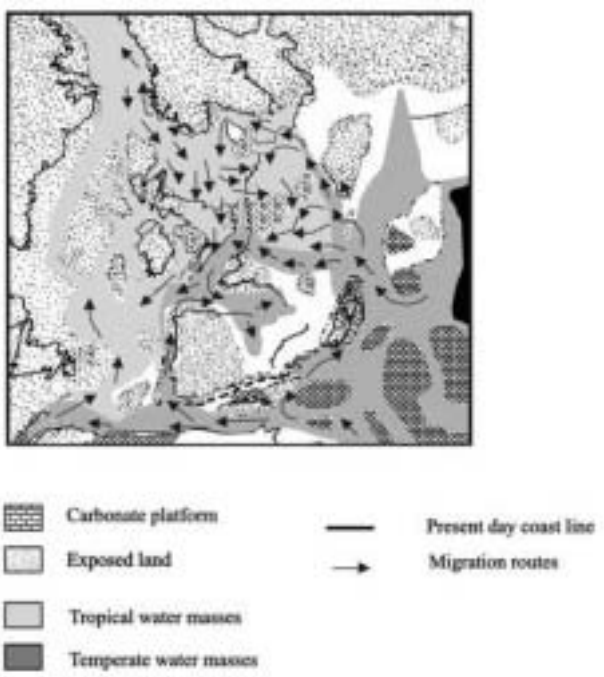

Fig. 5. Ostracod migration routes during the Early Jurassic palaeogeographical reconstruction modified from Scotese (2001).

Conclusions

The Early Jurassic was a time of an important marine faunal innovation that gave rise to the taxonomic prominence of several groups of microfossils that played a major role in the early Jurassic oceans. Ostracoda are regarded as one the most important fossil groups for the palaeobiogeography of the Early Jurassic, because they are characterized by being more cosmopolitan in distribution than other important fossils, such as ammonoids or bivalves, which improves our knowledge of Early Jurassic palaeobiogeography, palaeoceanography and palaeoclimatology. The faunal similarity among several regions of the European Epicontinental Sea, Tethys and Easter Panthalassa oceans illustrates the division of the European Epicontinental Sea–Western Tethys area into faunal regions. The cluster analysis showed an east-west splitting up along the North Sea during the Hettangian; between British and central European basins (French and German basins) during the Sinemurian, and between German and French basins during the Pliensbachian. At the beginning of Toarcian, the

boundary moved westward, falling apart the Western European Epicontinental Sea assemblages from the rest of European ostracod assemblages. The distributional limits of ostracod assemblages are set by its ecological attributes and historical factors (a certain water temperature control, sea-level changes, adjustment in physical barriers and changes in ocean circulation). In the present paper, the study of Early Jurassic ostracod palaeobiogeography and their palaeoecological requirements of the different types of Ostracoda under consideration allows us to explain the similarities among the ostracod faunas from Western European, Tethyan, South American and Australian basins.

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